A NEW SEX-LINKED CHARACTER IN DROSOPHILA.

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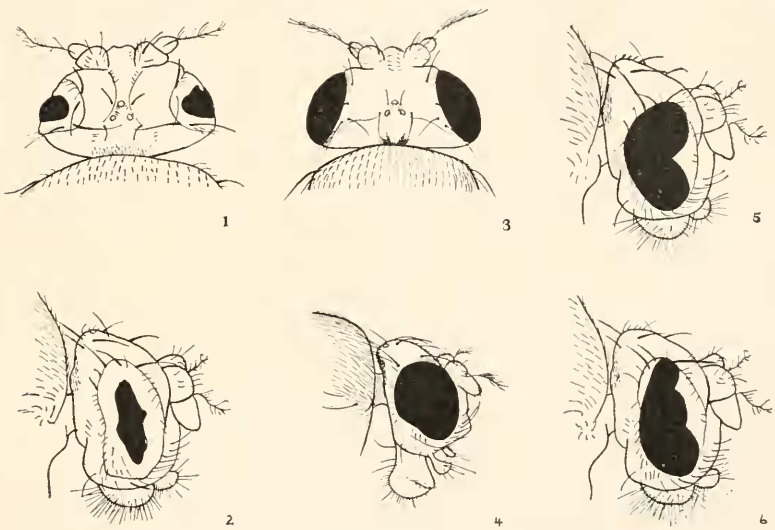
A new sex-linked character (Figs. 1 and 2) recently appeared in *Drosophila ampelophila* in an experiment involving rudimentary and long-winged flies with normally shaped eyes (Figs. 3, 4). The new character "barred" eye appeared in a single



Figs. 1 and 2. Pure barred (male) above and from the side.
Figs. 3 and 4. Normal eye (side view smaller fly).
Figs. 5 and 6. Two heterozygous eyes, both in side view.

male. The ommatidia are reduced in number and are restricted to an area shaped like a vertical bar or band, the edges of which are more or less irregular in shape.

Barred Eye by Normal Eye.

When the barred male was bred to normal-eyed females, the F_1 generation showed the barred eye in the females only (Figs. 5 and 6), the males being normal. This is what would be expected if the new character is sex-linked and dominant. The

F_2 generation (Table I.) with class ratios 1 : 1 : 1 : 1 is consistent with this expectation. In the following analyses *Br′* is the factor for the dominant barring and *br′* is its recessive normal allelomorph.

TABLE I.

P_1 Normal ♀, *X br′* — *X br′*.
Barred ♂, *X Br′* — ——.

F₁ Females.	F₁ Males.
{*X br′* / *X Br′*}	{*X br′* / ——}
Barred ♀.	Normal ♂.
570	565

Gametes of F_1 barred ♀, *X br′*—*X Br′*.
Gametes of F_1 normal ♂, *X br′*— ——.

	F₂ Females.		F₂ Males.	
	{*X br′* / *X br′*}	{*X Br′* / *X br′*}	{*X br′* / ——}	{*X Br′* / ——}
No.	Normal ♀.	Barred ♀.	Normal ♂.	Barred ♂.
2	170	136	158	122
3	160	140	142	140
4	155	124	154	119
5	92	105	91	79
6	81	58	87	63
7	112	88	82	83
8	102	86	87	93
9	104	84	92	89
10	87	72	84	90
Total.....	1,063	893	977	878

The barred females of the above F_2 generation were heterozygous in barring, and, when mated to their barred brothers, gave an equal number of barred and normal sons (Table II.).

TABLE II.

Gametes of F_2 barred ♀, *X Br′*—*X br′*.
Gametes of F_2 barred ♂, *X Br′*— ——.

F₃ Females.	F₃ Males.	
{*X Br′* / *X Br′*} {*X br′* / *X Br′*}	{*X Br′* / ——}	{*X br′* / ——}
Barred ♀.	Barred ♂.	Normal ♂.
236	106	123

The original barred male was crossed to his daughters (F_1 ♀♀, Table I.) and as expected the results (Table III.) were similar to those of Table II.

Table III.

Gametes of F_1 barred ♀, *X br′—X Br′*.
Gametes of P_1 barred ♂, *X Br′*— ——.

Females.		Males.	
{*X Br′* / *X Br′*	{*X br′* / *X Br′*	{*X br′* / ——	{*X Br′* / ——
Barred ♀.		Normal ♂.	Barred ♂.
281		159	140

In the experiments recorded in Tables II. and III. it was noticed that the barring was of two kinds: (1) A very narrow bar (Figs. 1 and 2) which appeared in all barred males, and in about one half of the double class of barred females, and (2)

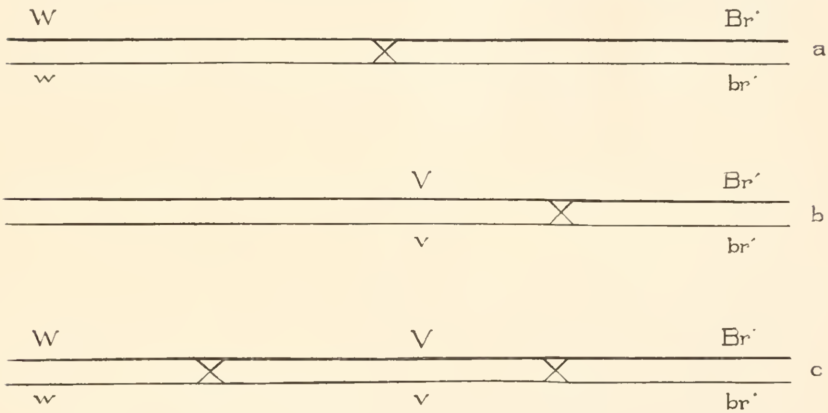


Diagram 1. (*a*) Showing loci of white (*w*) and barred (*br′*) in sex chromosomes of heterozygous female, with the loci of their normal allelomorphs. Crossing over is indicated by the *X* between the lines. (*b*) Ditto for vermilion and barred. (*c*) Ditto for white, vermilion, and barred.

a bar not so narrow which was present in the rest of the females. The loss in the latter case was mainly on the anterior edge and was especially noticeable as a single notch, or two notches, giving the eye a decided heart shape (Figs. 5 and 6). Here also the ommatidia are disturbed from their regular geometrical arrangement, and converge in rows to the notch. The difference in the narrow and broad bars is due to a difference in zygotic composition for, as will be described later, breeding tests have shown that invariably the broader types are heterozygous in barring (*Br′ br′*). When the narrow bar females were bred to barred males all the offspring were narrow barred. This stock has since bred true.

Red-barred Eye by White Normal Eye.

The original barred male was crossed with white-eyed females, with the results given in Table IV. The F_1 ♀ ♀ were red barred, and the F_1 ♂ ♂ were white normal, since white is a sex-linked character. The F_2 generation consisted of four classes, red barred, white barred, red normal, white normal, with an equality of males and females in each. The ratios of the four classes will be discussed later. In the following analyses, *w* is the factor for the recessive white (sex-linked) and *W* is its normal allelomorph (red).

Table IV.

P_1 White normal ♀, *X w br′*—*X w br′*.
Red-barred ♂, *X W Br′*— ——.

F_1 Females.	F_1 Males.
{ *X w br′* / *X W Br′*	{ *X w br′* / ——
Red Barred ♀.	White Normal ♂.
483	440

Gametes of F_1 barred ♀ *X w br′*—*X W Br′*—*X w Br′*—*X W br′*.
Gametes of F_1 white ♂—*X w br′*. — ——

	F_2 Females.				F_2 Males.			
	X w br′, *X w br′*,	*X W Br′*, *X w br′*.	*XwBr′*, *Xwbr′*.	*X W br′*, *X w br′*.	*X w br′*, ——	*X W Br′*, ——	*X w Br′*, ——	*X W br′*, ——
No.	White Normal ♀	Red Barred ♀.	White Barred ♀.	Red Normal ♀.	White Normal ♂	Red Barred ♂.	White Barred ♂.	Red Normal ♂.
101	72	84	31	43	86	75	46	71
102	74	58	41	53	65	60	55	52
103	62	81	40	47	57	66	43	52
104	45	35	29	36	21	41	28	30
105	46	58	30	42	35	48	30	46
106	26	44	18	21	24	27	20	29
107	32	44	23	22	25	32	15	19
108	35	43	27	32	31	58	33	45
109	34	41	25	36	31	38	27	39
Total...	426	488	264	332	375	445	297	383

The white heterozygous barred females (F_2 above), bred to their white barred brothers, gave the expected proportions (Table V.).

TABLE V.

Gametes of F_2 white barred ♀, *X w Br′—X w br′*.
Gametes of F_2 white barred ♂, *X w Br′*— ——.

No.	F_3 Females. { *X w Br′*, *X w Br′*, { *X w br′*, *X w Br′* White Barred ♀ ♀.	F_3 Males. { *X w Br′*, —— White Barred ♂.	{ *X w br′*, —— White Normal ♂.
a.	198	118	105
b.	224	116	101
Total	422	234	206

By mating together white narrow barred females (homozygous), and white barred males from the above experiment, a white barred stock was obtained which has since bred true.

The original mutant male was mated to his daughters (F_1, Table IV.) and gave the expected proportions (Table VI.).

TABLE VI.

Gametes of F_1 red barred ♀, *X w br′—X W Br′—X W br′—X w Br′*.
Gametes of P_1 red barred ♂, *X W Br′* — ——

Females.	Males.			
Red Barred ♀.	Red Barred ♂.	White Normal ♂.	White Barred ♂.	Red Normal ♂.
240	63	52	50	43

RED BARRED EYE BY VERMILION NORMAL EYE.

The original barred male was mated to vermilion eyed females with the results given in Table VII. As in the two previous cases the barred character was dominant and sex-linked, appearing in the F_1 generation in the females only. The F_1 females, as expected, were red and the males were vermilion, since vermilion also is a sex-linked character. The F_2 generation showed the expected sex-linkage results with four classes: vermilion barred, red normal, vermilion normal, and red barred, with an equality of males and females in each class. The ratios of these four classes will be discussed later.

In the following analyses v is the factor for the recessive sex-linked character vermilion and V is its normal allelomorph (red).

Table VII.

P_1 Vermilion normal ♀, *X v br′—X v br′*.
Red barred ♂, *X V Br′*— ——.

F₁ Females.	F₁ Males.
X v br′	*X v br′*
X V Br′	———
Red Barred ♀.	Vermilion Normal ♂.
367	312

Gametes of F_1 red barred ♀, *X v br′—X V Br′—X v Br′—X V br′*.
Gametes of F_1 vermilion normal ♂, *X v br′*— ——.

	F₂ Females.				F₂ Males.			
	X v br′. *X v br′*,	*X V Br′*, *X v br′*.	*X v Br′*, *X v br′*.	*X V br′*, *X v br′*.	*X v br′*, ——	*X V Br′*, ——	*X v Br′*, ——	*X V br′*, ——
	Vermilion Normal ♀.	Red Barred ♀.	Vermilion Barred ♀.	Red Normal ♀.	Vermilion Normal ♂.	Red Barred ♂.	Vermilion Barred ♂.	Red Normal ♂.
201	315	229	70	95	248	202	80	88
202	284	270	90	102	313	234	82	92
203	250	247	79	103	271	222	68	68
204	93	89	35	24	95	83	34	33
205	99	111	32	38	110	99	45	40
206	72	100	31	31	81	98	20	22
207	108	97	40	57	112	76	43	56
208	141	102	37	46	97	105	36	28
209	125	108	26	28	98	88	26	26
Total...	1,487	1,353	440	524	1,425	1,207	434	453

The heterozygous vermilion barred females (F_2 above) were mated to their vermilion barred brothers and gave the expected ratios (Table VIII.).

Table VIII.

Gametes of F_2 vermilion barred ♀, *X v Br′—X v br′*.
Gametes of F_2 vermilion barred ♂, *X v Br′*— ——.

	F₃ Females.	F₃ Males.	
	{*X v Br′*, *X v Br′*. {*X v Br′*, *X v br′*.	{*X v Br′*, ———	{*X v br′*, ———
	Vermilion Barred ♀.	Vermilion Barred ♂.	Vermilion Normal ♂.
a.	243	131	124
b.	278	125	169
Total...	521	256	293

By mating vermilion narrow barred females (homozygous) to their vermilion barred brothers, from the above experiment, vermilion barred stock was obtained which has since bred true.

The original male was mated to his daughters (F_1 Table VII.) and gave the expected proportions (Table IX.):

Table IX.

Gametes of F_1 red barred ♀, *X v br′—X v Br′—X V Br′—X V br′*.
Gametes of P_1 red barred ♂, *X V Br′*— ——.

Females.	Males.			
Red Barred ♀.	Red Barred ♂.	Vermilion Normal ♂.	Vermilion Barred ♂.	Red Normal ♂.
124	37	48	18	18

The Linkage of the Factor for Barred Eye.

Since the character barred is sex-linked it follows the sex chromosomes. It remains to determine its linkage with other sex-linked factors. Red barred males bred to white normal females gave in the F_2 generation (see Table IV.) the following results:

	White Normal.	Red Barred.	White Barred.	Red Normal.
♀	426	488	264	332
♂	375	445	297	383
Total.....	801	933	561	715

The non-cross over classes are red barred and white normal. The cross over classes are white barred and red normal (Diag. 1*a*). These two categories gives 42.8 per cent. crossing over.

In order to determine the linkage of barred to another sex-linked factor, viz. vermilion; red barred males were bred to vermilion normal females. The F_2 generation (see Table VII.) gave the following results:

	Vermilion Normal.	Red Barred.	Vermilion Barred.	Red Normal.
♀	1,487	1,353	440	524
♂	1,425	1,207	434	453
Total.....	2,912	2,560	874	977

The percentage of crossing over in the above case is 25.3 per cent. Diag. 1*b*.

Earlier experiments (Sturtevant, '13) have shown that there is about 30.7 per cent. of crossing over between white and vermilion. Since there is 25.3 per cent. crossing over between vermilion and barred the factor for barred must lie close to white (approximately 5.4) or else very far from white. That the latter is the case is shown by the large percentage of crossing over between white and barred (42.8 per cent.).

Other work done in this laboratory, largely as yet unpublished, shows that, when distances as long as this between white and barred are involved, the chromosomes often break at two points and re-unite. As a result of this double-crossing over, the non-cross over classes are increased and the cross over classes are diminished (Diag. 1*c*). The amount by which the percentage 42.8 is less than the percentage 30.7 + 25.3 is therefore an indication of the amount of double crossing over that has occurred. Sturtevant ('13) has located certain factors on the *X*-chromosome. Vermilion (*B*) is given as 30.7. The experiments in this paper giving 25.3 per cent. crossing over between vermilion and barred enable us to locate the new factor barred approximately at 56 (30.7 + 25.3) (without considering the double crossing-over between white and vermilion or that between vermilion and barred).

Dominance.

In these experiments whenever flies were heterozygous for barring they showed the barring without exception. In this sense the dominance is *constant*, in that a fly which fails to show the barring cannot transmit it. As was stated before the homozygous females have a narrower bar than the heterozygous females. That it is possible to pick out at sight the two different flies is verified by the following experiments.

P_1 Broad Barred ♀ (Heterozygous) by Barred ♂.

F_1	Barred ♀.	Barred ♂.	Normal ♂.
46	80	31	52
47	119	71	72
49	138	80	81
50	101	50	65
51	101	50	56
52	127	75	63
62	94	55	55
65	107	62	48
Total	867	464	492

P_1 Narrow Barred ♀ (Homozygous) by Barred ♂.

F_1.	Barred ♀.	Barred ♂.
90	65	60
91	43	35
56	86	76
58	101	117
60	118	119
64	90	94
Total	503	501

P_1 White Broad Barred ♀ (Heterozygous) by White Barred ♂.

F_1.	White Barred ♀.	White Barred ♂.	White Normal ♂.
146	62	30	27
147	86	36	39
151	88	37	44
152	69	31	23
Total	305	134	133

P_1 White Narrow Barred ♀ (Homozygous) by White Barred ♂.

F_1.	White Barred ♀.	White Barred ♂.
148	81	72
149	83	78
150	45	51
153	105	95
154	63	60
157	38	47
Total	415	403

P_1 Vermilion Broad Barred ♀ (Heterozygous) by Vermilion Barred ♂.

F_1	Vermilion Barred ♀.	Vermilion Barred ♂.	Vermilion Normal ♂.
249	57	23	29
256	84	39	42
257	67	45	36
258	87	39	37
Total	295	146	144

P_1 Vermilion Narrow Barred ♀ (Homozygous) by Vermilion Barred ♂.

F_1	Vermilion Barred ♀.	Vermilion Barred ♂.
246	67	72
247	30	39
248	52	46
250	42	37
253	43	50
254	48	46
Total	282	290

Viability.

In the foregoing experiment where an equality of barred and normal was expected, it is evident that the mutant character is almost as viable as the normal. For this reason it should prove valuable for further work on linkage. In the experiments in which no linkage is involved, there are 4,671 barred among 9,578 flies. The percentage of barred is 48.7 where 50 is expected. Where the experiments involving linkage are included, the barred flies total 9,767 out of 20,240 and the percentage is 48.2. The relative viability of white and barred appears in those experiments in which both were raised under the same conditions as 45.4 per cent. to 49.9 per cent. The relative viability of vermilion and barred was 51.7 per cent. to 46.8 per cent.

Conclusion.

Barred eye—a new sex-linked character—appeared in *Drosophila* in a single red-eyed male fly and its dominance is constant over the normal eye. The broad bar of the heterozygous females distinguishes them from the homozygous ones with a narrow bar. The viability of the stock makes it valuable for linkage experiments.

By taking the percentage of cross overs as an indication of distance on the chromosome, we can place the factor for barred approximately at 56.

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